A HOLE IN A TENT OR HOW TO EXPLORE INSECT ABUNDANCE AND DIVERSITY

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Every scientist likes to think that his contribution will be incorporated into the text books and that his name will be remembered. But theories and hypotheses can be tested and shown to be wrong, and data can be reworked and reinterpreted to show that the researcher missed the point, collected the wrong information, or performed the wrong experiment. There is, however, one activity open to the biologist which ensures that his name is recorded and remembered: discovering a new, undescribed species of plant or animal and having it named after him. Even if it later turns out the species has already been described, perhaps in an unlikely journal or in an unfamiliar language, the name is preserved in the archives of synonymy.

In 1964 and 1965 I collected a sample of Ichneumonidae in a Malaise trap sited in the garden of the house I lived in at Kampala, Uganda. The sample was sent to Henry Townes and in it he found 88 males and 41 females of a genus and species new to science. The genus was described as *Owenus* and the species as *Owenus minor* (Townes 1970). The original drawing of *Owenus minor* is reproduced in Fig. 1. Further collecting in Africa and examination of collections of ichneumons in museums has revealed at least 44 species of *Owenus*, but to date only three have been described.

A specialist in ichneumons would not be astonished to hear of the discovery of a new genus with more than forty species from the heart of Africa, but an ecologist without special knowledge of ichneumons is at once impressed and humbled by the extraordinary diversity of the family with more undescribed than described species in some areas. I am of course thrilled to have a genus named after me. I may regret that the rules of nomenclature do not allow the name *Owenus* to be used again for a more spectacular animal, a new shark or parrot perhaps, but in the event I am unlikely to discover these.

The genus *Owenus* was discovered as a consequence of taking routine samples of insects in a Malaise trap to try and detect seasonal changes in abundance and diversity at a site near the equator where seasonal changes in weather are not marked. The value of the Malaise trap as a means of assessing the insect fauna of a site is beginning to be appreciated and various designs of trap are in wide use. I was first introduced to the Malaise trap in 1960. Henry Townes suggested that it might be interesting to operate one on Evans Old Field on the Edwin S. George Reserve, Michigan, an intensively studied site where, it was believed, the insect fauna was well known. The trap dramatically increased the species list, especially of Diptera and the smaller Lepidoptera (Evans and Murdoch 1968), and also demonstrated that various types of quantitative information could be obtained (Evans and Owen 1965). I have used Malaise traps ever since 1960 and in this paper I shall review the kinds of ecological information that can be obtained from them. A partial bibliography of the Malaise trap is given by Steyskal (1981). This is valuable but it does not indicate how the trap can be used as an effective sampling device.

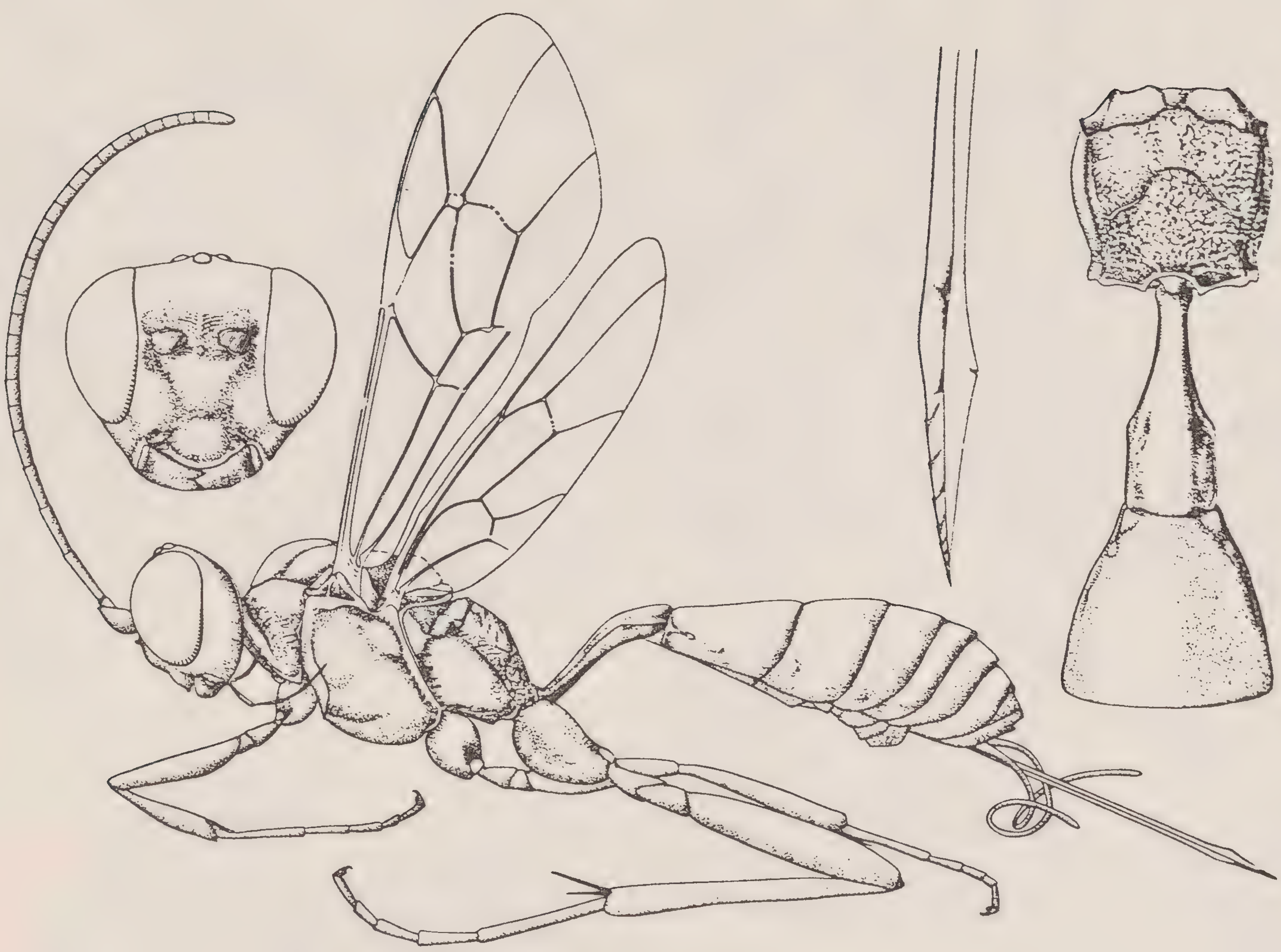

Fig. 1. **Owenus minor** Townes

A SIMPLE IDEA

There is no doubt that Rene Malaise discovered what has since become known as the Malaise trap. In his account (Malaise 1937) of a new insect trap he wrote, "During my extensive travels I have repeatedly found that insects happened to enter my tent, and that they always accumulated at the ceiling-corners in vain efforts to escape at that place without paying any attention to the open tent-door. On one occasion one of the upper tent-corners happened to have a small hole torn in the fabric, and through this hole all the insects pressed their way and escaped. Later the idea occurred to me, that, if insects could enter a tent and not find their way out, and always persistently tried to reach the ceiling, a trap made as invisible as possible and put up at a place where insects are wont to patrol back and forth, might catch them much better than any tent and perhaps better than a man with a net, as a trap could catch all the time, by night as well as by day, and never be forced to quit catching when it was best because dinner-time was at hand." Malaise then described how he used the new device in Burma and what an extraordinary number and variety of insects it produced. He also made a prediction and wrote, "For students interested in a statistical survey of the insect-fauna of a particular region, this trap may prove most useful, and it is possible that it might also be used with success in orchards to decimate insect-pests." Despite Malaise's enthusiasm for his discovery, the idea was not taken up by many entomologists until Henry Townes, with customary precision and attention to detail, explained exactly how to make a trap (Townes 1962). This particular design, open on four sides, was the

one I used in Michigan and later in Uganda. It was rather time-consuming to construct and soon after a simpler type, open on two sides, was invented (Townes 1972a), I adopted it and have used it ever since.

A suitably-sited Malaise trap catches an extraordinary number and variety of insects. Since no attractant is used, the trap samples only those individuals that enter its air space and thus accurately monitors what is going on in that space. If a trap is left at the same site for a whole season an enormous amount of information is obtained. It is possible to compare sites and to compare seasons, but impossible to do the necessary taxonomic work on all the insects collected. The trap that caught the 129 specimens of *Owenus minor* in the Kampala garden caught in one year an estimated 113,538 insects belonging to 13 orders. The insects were not counted out individually and the estimate was obtained by counting the insects in 52 48-hour samples taken once a week throughout the year. I have never attempted to estimate the number of insects taken in a year in a Malaise trap operated in a temperate climate. I suspect the figure is just as high with, of course, much more conspicuous seasonal changes in numbers.

Rene Malaise's observation of what insects did when they reached the hole in the top of his tent resulted in a significant break-through in the sampling of flying insects. Henry and Marjorie Townes have together been responsible for what might be called research and development in the construction and operation of Malaise traps; indeed there was a time when the traps almost became known as Townes traps.

Nearly everywhere I have used Malaise traps I have taken out the Ichneumonidae and sent them to the American Entomological Institute. My specimens are always collected and preserved in 70% alcohol and Marjorie Townes has pinned and dried them. Henry Townes then tabulated the species. One result of this collaboration is that the American Entomological Institute received some interesting and valuable specimens; another is that the tabulations of numbers and species have raised some questions about comparisons of temperate and tropical species diversity.

ICHNEUMONID DIVERSITY AT FOUR SITES

Ichneumonids tend to occur as individuals. Rarely is a species common and samples taken in Malaise traps invariably contain many species. With an estimated 60,000 species in the world, more than all the vertebrates put together (Townes 1972b), they are an excellent group for comparisons of species diversity at different sites. Numerical information on diversity is available from four samples, two tropical and two temperate. The first sample obtained was from the garden at Kampala, Uganda, and the results were published in Owen and Chanter (1970). Next came a similar sample from a garden at Freetown, Sierra Leone (Owen 1971). Then followed two temperate samples, one from a garden in Leicester, England (Owen, Townes and Townes 1981), the other from disturbed land along a small stream in Skåne, Sweden (Owen and Owen 1974). The four sites are not of course identical. Kampala and Freetown are at opposite sides of tropical Africa, the garden at Leicester is decidedly suburban, while the Skåne site is not a garden at all. But each was obtained by using Malaise traps for 12-month periods, and

the only assumption made is that the traps used did not select for either rare or common species.

The four samples are summarized in Table 1. The information theory index of diversity, H, enables comparison of species diversity. The values of H for Freetown and Leicester are not significantly different but all the other paired samples are different from one another at the 1% level. Particularly interesting is the fact that H is significantly smaller for the Kampala sample than for the Leicester and Skåne samples, and is smaller for the Freetown sample than for the Skåne sample.

TABLE 1. Two tropical and two temperate samples of Ichneumonidae compared. From Owen and Owen (1974).

	Sample size	Species	Diversity index, H, and s.e.	Species taken once	% commonest species
Kampala	2,268	293	4.524 ± 0.032	116	10.1
Freetown	1,979	319	4.934 ± 0.029	117	4.9
Leicester	2,495	326	4.937 ± 0.024	122	3.2
Skåne	10,994	758	5.481 ± 0.014	203	5.5

In Table 1 no special attention should be paid to the actual sample sizes nor to the number of species in each sample, except to note that at all four sites the number of species is very high indeed. More relevant is that at all sites the number of species taken once only is consistently high and that there are no really common species. The four samples are rather similar and there is not the expected higher diversity in the two tropical samples.

Every ecologist knows that the diversity of species of plants and animals is much higher in the tropics than in the temperate regions, and that there is a latitudinal gradient of decreasing diversity from the equator towards the polar regions. This is certainly true of trees, birds, butterflies and a few other groups that have been well studied, but on the basis of the figures in Table 1 is not true of the Ichneumonidae where all four samples are of the typical tropical type: many species but none particularly common. What is the explanation?

First, a word of caution because it is obviously necessary to obtain more comparable samples of Ichneumonidae to ascertain whether what has thus far been discovered is a general phenomenon. It would also be valuable to have temperate and tropical samples of other Hymenoptera that are parasitoids of insects. It might be that in the tropics other families of parasitoids, including dipterous families, are more diverse than in the temperate regions.

Another problem is seasonal heterogeneity in samples taken over an entire year. Ecological conditions are constantly changing and there is the possibility that the cumulative number of species is higher in a tropical environment than in a temperate one. In view of this I have re-examined the Kampala and Leicester samples to see how many species were added each month during the sampling period.

The Kampala year started in July 1964 when 81 species were taken. In August there were 58 species, 53% of which did not occur in July. Of the 47 species taken in September, 36% were new to the sample. Thereafter the percentage of species added until April 1965 varied between 21% and 29% per month, which suggests a relatively stable rate of addition of species. In May 1965, 59 species were taken, 15% of them additions, and in June, the last month of the sampling period, there were 57 species, 12% of them additions to the total sample. As expected the rate of addition was highest in the first few months; it then seemed to stabilize, and in the last two months began to fall. Clearly it would have been worth continuing sampling for a few more months.

The Leicester year started in January 1972 but no ichneumonids were caught until the first warm weather in March when three species were taken. In April there were six species, three of them additions. And then 62 species were taken in May, 92% of them additions which, of course, is a simple sampling effect resulting because so few species had been taken in the previous months. By June ichneumonids were much more abundant and 116 species were taken, 69% of them additions. In July 152 species were taken, 51% of them additions, while in August, the best month, there were 183 species, 33% additions. Thereafter the number of species fell off with 18% added in September, 14% in October and only 4% in November when only 25 species were taken as the season was almost over. None was taken in December.

It is not easy to compare seasonal heterogeneity at the two sites because at Kampala ichneumonids occur all year round with no obvious peaks of abundance and diversity while at Leicester both abundance and diversity are strongly seasonal. It is, however, obvious that at both sites the species composition changes markedly from month to month. Ichneumonids were tabulated from the Leicester trap for the following year, 1973, and a further 129 species were added; only 255 of the 455 species in the two years occurred in both years (Owen, Townes and Townes 1981).

When the two tropical and temperate samples were first compared (Owen and Owen 1974) it was suggested that the similarity between them is because ichneumonids are niche specific rather than host specific. This suggestion implies that there are no more niches for ichneumonids in the tropics than in temperate regions, and is derived from a general statement in Townes (1972b) for the family as a whole. Townes (1972b) writes, "Ovipositing adult parasites are attracted not to hosts, but first to ecological niches and after that to whatever hosts might be present. Host species that do not occur in the micro-habitat of the exploring female parasite are never attacked . . . A parasite of pupae in leaf rolls will not attack pupae in cracks in the bark or on the ground. Very seldom do parasites attacking hosts on grasses turn to hosts on forbs, or do parasites of hosts on conifers attack hosts on

deciduous trees. The micro-habitat of the ovipositing female can be very specific, but within its own micro-habitat it may attack a large variety of hosts. Thus, to say that a parasite attacks a particular host is an incomplete statement. One should say that a parasite attacks hosts in a certain micro-habitat, among which is the species in question." This statement is not based on detailed observations of ichneumonids seeking micro-habitats and hosts in the wild but from rearing records. As Townes (1972b) points out, field observation is virtually impossible because most ichneumons are difficult to identify to species in the field.

I am convinced that the Ichneumonidae are an established exception to the rule of increasing species diversity from high to low latitudes, and I am equally convinced that the rule may not be as general as has been widely assumed. The difficulty is that most studies of tropical versus temperate diversity have been made on relatively few groups of conspicuous and well-known organisms like birds and trees. What is needed are comprehensive data for other groups such as non-woody flowering plants which (excluding epiphytes) might turn out to be just as diverse in temperate as in tropical forest; noctuid moths might also repay study.

MONITORING BUTTERFLY ABUNDANCE

Perhaps because there are only about sixty species, much interest and concern is directed towards Britain's butterfly fauna. Most agree that many species have declined in recent years and blame modern farming methods and the replacement of deciduous woodland with plantations of non-native conifers. One problem is that every so often there is a good year for butterflies which casts doubt on whether farming and forestry have had the repeatedly claimed bad effects on the fauna. Another problem is that butterfly abundance is difficult to monitor. Various techniques have been tried, including transect counts and capture-mark-recapture, but with limited success.

The Malaise trap in the Leicester garden has been operated at the same site for ten consecutive years and has yielded a wealth of information on annual and seasonal variation in the numbers and diversity of many groups of insects. As each year is completed the information obtained becomes more and more valuable. It is easy to see that there is no such thing as a normal year and that the populations of many of the commoner species are subject to enormous fluctuations in numbers.

Twenty-one species of butterflies have been recorded in the Leicester garden. Numbers vary from year to year but since the garden butterfly community is highly mobile (few species actually breed there) it is difficult to assess whether there are good and bad years. The Malaise trap has taken relatively few butterflies but numbers are sufficient to demonstrate annual variations in butterfly activity, as shown in Table 2.

Thirteen species were trapped. The annual total of individuals varied from 4 in 1981 to 172 in 1973. The trap confirms that numbers vary markedly from year to year and it is probably an effective monitor of butterfly activity which could be useful in more natural habitats where both numbers and the variety of species are higher.

TABLE 2. Annual variation in numbers of butterflies in a Malaise trap in a garden at Leicester, England, 1972-1981.

	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981
Thymelicus sylvestris	-	-	-	-	1	-	-	-	-	-
Ochlodes venata	1	1	-	-	-	-	-	-	-	-
Gonepteryx rhamni	-	1	1	-	-	-	-	-	-	-
Pieris brassicae	2	9	12	20	2	-	1	7	4	-
P. rapae	24	115	41	58	44	5	33	13	10	2
P. napi	10	23	20	14	12	6	25	6	8	2
Anthocharis cardamines	-	-	-	-	-	1	2	1	3	-
Lycaena phlaeus	-	-	-	3	-	-	-	-	2	-
Vanessa atalanta	-	1	-	-	2	1	-	-	-	-
Aglais urticae	3	18	3	2	1	-	-	-	-	-
Inachis io	1	2	-	2	1	-	-	-	-	-
Lasiommata megera	1	1	-	4	6	-	-	-	-	-
Maniola jurtina	1	1	-	-	10	1	-	-	-	-
Total	43	172	77	103	79	14	61	27	27	4

In the tropics Malaise traps catch substantial numbers of butterflies. The trap in the Kampala garden took 3661 in a year and the trap in the Freetown garden took 899. The specimens were separated into families, but in most cases not into species, but it was clear that had there been time to do the necessary taxonomic work an impressive picture of seasonal changes in abundance and diversity would have emerged.

TWO TRAPPING METHODS COMPARED

Malaise traps take large numbers of small moths but at most sites rather few of the larger species are caught. On 22 June 1961 the trap operated on Evans Old Field in Michigan caught a specimen of the medium-sized sphingid, *Xylophanes tersa*. The species had not appeared in mercury vapor light traps operated in the vicinity and, moreover, had only once before been recorded from Michigan (Moore 1955). I put this down as an interesting record and thought no more about it; after all to sample Sphingidae the most effective method is to use a light trap.

Between October 1966 and May 1968 I operated a mercury vapor light trap in the garden at Freetown, Sierra Leone, and caught 6619 Sphingidae of 52 species. Four Malaise traps were operated continuously (day and night) in the same area between January 1967 and May 1968 and produced 221 Sphingidae of 29 species. Full details of these two samples are given in Owen (1969a).

The relative frequency of the species of Sphingidae in the two samples is markedly different. All but two of the species caught in the Malaise traps were taken in the light trap. One is a day-flyer and would therefore not be expected in the light trap. For nearly all the commoner species the light trap was much more effective than the Malaise traps. The Malaise traps had therefore contributed rather little to the species list for the area.

Both samples contained a few common species and many relatively rare species enabling α, the logarithmic index of diversity (Fisher, Corbet and Williams 1943) to be calculated. The value of α =diversity for the light trap sample is 7.9 ± 0.4 and the value for the sample from the Malaise traps is 8.9 ± 1.1. The two values are not significantly different. Hence despite totally different trapping methods and different relative frequencies of species, the values of overall diversity for the site are not different. In this instance one trapping method would have sufficed to obtain a diversity estimate for the local Sphingidae.

DETECTING INSECT MOVEMENTS

Many insects periodically undertake mass movements from one place to another, often in response to a change in weather or a failure in the local food supply, or both. The meadow spittlebug, *Philaenus spumarius*, invades Evans Old Field when surrounding alfalfa fields are mown, an action which quickly deprives the bugs of food (Evans and Lanham 1960). Malaise traps are highly effective monitors of insect movements, often picking up the beginnings of an influx into an area before it has been noticed by even the most observant entomologist.

The ten years of Malaise trapping in the Leicester garden have provided numerous examples of movements into the area, particularly of Syrphidae (Owen 1981), Coccinellidae, and certain species of moths. Nearly always the weekly samples from the trap gave the first indication of a movement into the garden which, for certain species in certain years, later produced immense numbers. The Leicester trap is particularly effective at catching Coccinellidae. The annual catches of three of the nine species recorded in the trap are given in Table 3.

Adalia 2-punctata is normally the commonest coccinellid in the garden where both larvae and adults are predators of aphids feeding chiefly on woody shrubs and trees. As shown in Table 3, the numbers taken each year vary, but not conspicuously, except in 1979 when the population collapsed and 1981 when again the species was not common. In this species there is no evidence of influxes and the fluctuations in numbers are believed to be the result of events in the garden itself. It is known, for example, that numbers of certain species of aphids vary considerably and this alone could affect the survival rate of both larval and adult *A. 2-punctata*.

TABLE 3. Annual fluctuations in numbers of three species of Coccinellidae in a Malaise trap in a garden at Leicester, England, 1972-1981.

	Adalia 2-punctata	*Coccinella 7-punctata*	*Coccinella 11-punctata*
1972	168	4	2
1973	324	-	-
1974	155	-	1
1975	424	121	108
1976	346	564	98
1977	359	86	12
1978	239	33	2
1979	30	17	-
1980	129	18	-
1981	53	2	-

For the first three years, *Coccinella 7-punctata* was rare (1972) or absent (1973 and 1974) in the Malaise trap catches. This species is more characteristic of open country where larvae and adults feed on aphids on herbaceous plants, including field crops. In the first two weeks of August 1975 large numbers entered the garden during a period of exceptionally dry weather. It was presumed at the time that this influx was caused by a crash in numbers of aphids in nearby fields, perhaps brought about by the dry weather. The influx was followed by successful overwintering in the garden and considerable numbers in the trap in the early part of the 1976 season. Then in the third week of July 1976 even larger numbers came into the garden and stayed on to overwinter. This influx occurred when conditions were particularly dry and again it was believed to have originated from surrounding fields. Indeed the 1976 summer was the driest and sunniest in southern and central England for about 250 years, a fact which was repeatedly shown in Malaise trap records of rare and unusual insects which, presumably, were moving about more than usual. From 1977 onwards there were no further influxes and the relatively high numbers (compared to 1972-1974) are attributable to the species breeding in the garden. It was not until 1979 that the effects of the 1975 and 1976 movements into the garden had disappeared.

Coccinella 11-punctata is in Britain essentially a coastal species and in most years is rare or absent in the Leicester Malaise trap, as shown in Table 3. In 1975 large numbers entered the garden at the same time as the influx of *C. 7-punctata*, some of them, it was believed, having travelled

considerable distances. They did not breed and by 1977 had become rare. Only two were recorded in the trap in 1978, and none since.

The resident garden community of coccinellids consists essentially of *A. 2-punctata* and a sprinkling of five other species, including variable numbers of *Propylea 14-punctata* which may at times invade from surrounding woodland. The 1975 and 1976 influxes of *C. 7-punctata* and *C. 11-punctata* disrupted the community by altering the species composition. The Malaise trap faithfully timed and monitored these influxes in a way that would not have been possible by even the most careful observations.

QUANTIFYING INSECT MIGRATION

Every year the plusiid moth, *Autographa gamma*, arrives in Britain from the continent of Europe and breeds successfully. It is doubtful if it ever successfully overwinters in the wild at any stage of its development. Although direct evidence is scarce, it seems likely that substantial numbers of *A. gamma* fly south from Britain in autumn. Table 4 shows the date of first arrival of immigrant *A. gamma* and the number taken in the Malaise trap in the Leicester garden during ten consecutive years. As shown, the moth normally arrives in June; its early arrival in May 1976 can be attributed to the exceptionally dry weather in western Europe that year. Numbers fluctuate markedly: 1973 and 1975 were "good years", and 1981 was a very poor year. These figures confirm that numbers of *A. gamma* vary from year to year but they do not provide information on spring and autumn flight directions because the trap is not designed to separate insects entering from different directions.

TABLE 4. Date of first arrival and fluctuations in numbers of the migratory moth, *Autographa gamma*, in a garden at Leicester, England, 1971-1981.

	Date of arrival	Number taken in Malaise trap
1972	?	44
1973	16 June	233
1974	4 June	20
1975	30 June	155
1976	22 May	51
1977	25 June	37
1978	3 June	23
1979	10 June	17
1980	6 June	24
1981	16 June	4

Malaise traps that collect and separate insects arriving from different directions have been used to monitor Trichoptera flying up and down over a small stream in southern Sweden (Svensson 1974). The Malaise trap is of course an interceptor and there is no reason why suitable modified designs should not provide information on the flight directions of insects involved in long-distance migratory flights. Such traps have been designed and used to quantify flight directions taken by butterflies migrating through Gainesville, Florida (Walker 1978).

These traps are much larger than the light-weight trap designed by Townes (1972a). They are erected in places where butterflies are known to migrate and if run for a year provide information on numbers moving north and south. Thus Walker (1978) demonstrated a substantial southerly movement in authumn of the hesperiid, *Urbanus proteus*, and similar but less substantial movements of seven other species of butterflies. With so many butterflies flying south in autumn a return flight north in spring is to be expected, but except for a small movement of the nymphalid, *Precis coenia*, no evidence of this was obtained from the Malaise traps. As Walker (1978) points out, there may be several reasons why the northward flight was not effectively monitored by the Malaise traps.

The most obvious is that the northward flight involves many fewer individuals. Observations of migratory butterflies in many parts of the north temperate region suggest that almost invariably many more individuals are seen flying south in autumn than north in spring (Williams 1930). Another reason is that northward flights may tend to occur too high for the trap to intercept them. And a third reason is that an insect entering from the north has a greater chance of being trapped than one entering from the south. Insects move towards the light and since at Gainesville the sun has a southerly aspect, butterflies arriving from the north might have a greater chance of ending up trapped. Walker (1978) tested this possibility by comparing numbers of the non-migratory hesperiid, *Hylephia phyleus* , and found no statistical difference between north and south samples.

It is the ability of the Malaise trap to continually monitor, by day and night and in all weather, that makes it superior to most other trapping methods for flying insects. For assessing the volume of butterfly migration it is much easier to use a trap than to stand still for hours counting individuals as they fly past. Not all butterflies are immediately identifiable in the field and this is another reason why observation has its limitations.

UNDERSTANDING SEASONAL CYCLES IN EQUATORIAL VERTEBRATES

Kampala at 0° 20' N is an ideal place for the study of the seasonal breeding and migratory cycles of mammals and birds. The temperature changes little during the year, fluctuations in each 24-hour period being greater than seasonal changes, and daylength is effectively constant. Rainfall occurs in all months of the year with two seasonal peaks which, however, are not reliable. It is an extremely uniform climate but despite this most vertebrates that have been studied exhibit seasonality in their breeding or migratory cycles. Thus Mutere (1973) found seasonal peaks in the breeding of two species of insectivorous free-tailed bats, *Tadarida*, which are correlated to some extent with

seasonal changes in the amount of rainfall. He postulated that rainfall acted as a proximate stimulus for breeding and that variation in the availability of night-flying insects, particularly moths, is the chief ultimate factor. But alathough rainfall figures were easy to obtain, information on seasonal fluctuations in abundance of night-flying insects (the food of the bats) was unavailable, with the notable exception of the results from the Malaise trap in the Kampala garden. The trap indicated that during a year the mean number of moths caught per 24 hours varied between 196 (May) and 73 (August). This provided the only information on possible variation in moth abundance which could be correlated with bat breeding cycles.

Many insect-eating birds that breed in the Palearctic fly south in autumn and "winter" on or near the equator in Africa. There is much circumstantial and some experimental evidence that the stimulus to commence the southward migration is provided by decreasing daylength, decreasing temperature, and a progressive failure of the insect food supply. But how do these birds time the commencement of their return flight in February and March? On the equator daylength and temperature are effectively constant and could hardly act as stimuli for the birds to set off on the long northward flight back to the breeding areas.

Because of the apparent lack of a seasonal trigger, it was postulated for one species, the yellow wagtail (*Motacilla flava*), which in the northern winter is extremely abundant around Kampala, that there is an internal timer which (soemhow) is set to act at the correct time for the northward departure (Curry-Lindahl 1958, Marshall and Williams 1959). Evidence for the existence of an internal timer is based on a failure to find environmental stimuli that might trigger the start of the northward flight. Such evidence is to say the least rather unsatisfactory. The possibility that insect numbers on or near the equator fluctuate sufficiently on a seasonal basis to stimulate the return migration of the yellow wagtail was discounted (Marshall and Williams 1959) or ignored (Curry-Lindahl 1958).

Table 5 shows the mean number of insects per 48 hours in the Kampala Malaise trap for each month of the year starting July 1964. It also shows the actual rainfall for each month and the 10-year mean monthly rainfall. Monthly variations in insect numbers correlate better with the mean "expected" rainfall than with the actual rainfall, suggesting that in many species there is a built in cycle with the peak abundance at the best time of year, during and just after the annual rainfall peak. Yellow wagtails begin to leave Kampala in February, the least good month for insects, and continue to leave through March and early April, when insect numbers are increasing towards the May peak. Their departure thus occurs during the period of maximum change in the abundance of their potential food supply, and this itself could provide the necessary stimulus to migrate north.

The figures in Table 5 are based on only one year of Malaise trap sampling. Caution is therefore necessary in interpreting fluctuations in numbers as being sufficient to provide the stimulus for yellow wagtails (and other insectivorous birds) to set off for the north, but the possibility remains, especially as essentially the same evidence of fluctuations in abundance was obtained by sweep sampling on the Athi Plains near Nairobi, Kenya (Dingle and Khamala 1972).

TABLE 5. Seasonal fluctuations in insect numbers and rainfall, Kampala, Uganda, July 1964–June 1965. From Owen (1969b).

	Mean number of insects per 48-hour sample	Actual rainfall (mm.)	10-year mean rainfall, 1953-1962 (mm.)
July	669	24	51
August	480	85	111
September	452	206	98
October	399	135	121
November	436	140	115
December	527	216	96
January	458	15	64
February	196	73	53
March	668	139	139
April	1156	159	174
May	1176	50	95
June	790	10	61

I was not of course able to show that fluctuations in insect numbers directly affect the availability of food to the birds, but the existence of such fluctuations must be taken into account before the concept of the internal timer is accepted. My hypothesis makes fewer assumptions in the field of avian physiology than that of Curry-Lindahl (1958) and Marshall and Williams (1959) and for this reason alone it is to be preferred until more evidence is forthcoming.

THE HOLE IN THE TENT

I have been Malaise trapping for more than twenty years and I still find it absolutely compulsive, whether in some remote tropical place or in my own garden. Indeed the garden trapping, now in its eleventh year, has produced a quite extraordinary amount of information on the abundance and diversity of many groups of insects. It has also been exciting, even though nothing quite as unusual as *Owenus* has turned up, and the trap continues to produce new records of insects for this part of England.

I must acknowledge Rene Malaise's perception when he realized what was going on at the hole in the top in his tent. I acknowledge even more the efforts of Henry and Marjorie Townes in developing Malaise traps and for the enormous amount of taxonomic work they have put into my samples of Ichneumonidae and other parasitic Hymenoptera. It is an honor to dedicate this paper to Henry Townes on the occasion of his 70th birthday.

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